

## IMPACT OF RECURRENT FIRE ON ANNUAL PLANTS: A CASE STUDY FROM THE WESTERN EDGE OF THE COLORADO DESERT

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### ABSTRACT

Limited information exists regarding the impact of fire on annual plant composition in creosote bush scrub vegetation. The impact of recurrent fires on annual plants is even less understood. To investigate this matter, annual vegetation was sampled in a stand of creosote bush scrub in western Coachella Valley, California that had recently experienced two wildfires. The wildfires fragmented the once contiguous shrubland into three sections: unburned, once-burned, and twice-burned stands, all of which were separated by fuel breaks that contained each fire. For all three stands, annual plant cover and species richness were determined in the field, soil seed bank samples were collected and assayed in a glasshouse, and soil chemistry and physical properties were measured. We found that invasive annual grass cover was highest in the twice-burned stand and native annual plant cover was greatest in the unburned stand. Native annual species richness significantly decreased each time a stand burned resulting in low native annual plant diversity. Seed bank assays revealed that invasive annual grass germinants were orders of magnitude greater in the twice-burned stand compared with the other two stands. Lastly, soil total N, C, and soil pH were elevated in both burned stands. Overall, we found that recurrent fire can result in strong impacts to annual vegetation; however, the twice-burned stand was sampled only three years after burning while the once-burned stand was sampled 20 years after burning. Thus, longer-term fire effect studies plus replication with additional study sites are still needed to improve our understanding of how recurrent fire impacts annual plants.

Key Words: Diversity, feedback, grass/fire cycle, invasive plant, richness, seed bank.

Invasive grasses can alter the fire regime by increasing the frequency, intensity, extent, and seasonality of fire (Brooks et al. 2004). In creosote bush scrub vegetation of southern California, the invasive grasses are annuals that differ fundamentally from the native annual forbs that they displace. For example, unlike most native annual plants, invasive annual grasses senesce earlier and have persistent standing biomass throughout the dry season (Brooks 1999). One problematic result of grass invasion for creosote bush scrub is longer-lasting fine fuel that connects widely spaced shrubs (Brooks et al. 2004). In addition, invasive grasses can form higher density assemblages than native vegetation (Steers and Allen 2010), thus increasing the fuel packing ratio and consequently, fire intensity.

The primary foci of previous studies examining fire in desert shrublands of the Mojave and Sonoran Deserts have been on the impacts to perennial species. These studies have documented reductions in cacti and long-lived shrubs, such as *Larrea tridentata* Coville, and increases in relatively short-lived perennials (O'Leary and Minnich 1981; McLaughlin and Bowers 1982; Brown and Minnich 1986; Alford et al. 2005; Brooks and

Minnich 2006; Abella 2009; Abella 2010). However, most of these studies did not measure annual vegetation.

Previous studies that have focused on fire and desert annual plants documented post fire decreases in *Bromus madritensis* L. subsp. *rubens* (L.) Husn. and increases in *Schismus* spp. (either *S. arabicus* Nees, *S. barbatus* [L.] Thell., or both), which are both invasive annual grasses. These studies also documented little change in the abundance of the invasive forb, *Erodium cicutarium* (L.) Aiton, and either an increase or decrease in native annuals, depending on the species (Cave and Patten 1984; Brooks 2002; Esque et al 2010a, b; Steers and Allen 2011a). Native annual plant species richness has also been shown to decline in shrub understories after fire but no response was detected in interspace habitat (Brooks 2002). Besides these studies, little information exists on the impacts of fire on desert annual plants. Brooks et al. (2004) and Brooks and Esque (2002) warn that post fire increases in invasive annual grasses may promote recurrent fire, *sensu* the grass/fire cycle (D'Antonio and Vitousek 1992). However, documentation of the impact of recurrent fire on annual vegetation is lacking.

The goal of this study was to document the impact of fire on the annual plant community in creosote bush scrub that partially burned in 1988 and in 2003. The fire history of this study site

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resulted in an unburned, once-burned, and twice-burned stand. Our objective was to measure the response of invasive annual grasses and forbs to fire, and the impact of fire on native annual plants. We were especially interested in documenting the response of native annual plant species richness and diversity measures to recurrent fire, as this is relatively unknown. In addition to vegetation surveys, seed bank samples collected from the three stands were also assayed and soil parameters (nutrients, texture, and pH) were measured to provide additional insight.

## MATERIALS AND METHODS

### Study Area

The study site was located in Whitewater Canyon (33°56'50"N, 116°38'43"W) on the western edge of the Colorado Desert in Riverside County, California. Vegetation along the floor of Whitewater Canyon was composed of desert riparian and desert dry wash communities. Creosote bush scrub occurred throughout the valley bottom, upland of the riparian and wash areas. On steeper slopes of the canyon, *Encelia farinosa* Torr. was dominant. Coastal scrub shrubs, such as *Artemisia californica* Less. and *Salvia apiana* Jeps., were occasional on north and east facing hill slopes. Within unburned creosote bush scrub of the study site, perennial vegetation was about 21% cover (Steers and Allen 2011b). *Larrea tridentata* contributed about 10% cover, *Ambrosia dumosa* (A. Gray) W. W. Payne 6%, *Krameria grayi* Rose & Painter 3%, and the following species individually contributed less than 2% cover: *Psoralethamnus arborescens* (A. Gray) Barneby, *Ephedra californica* S. Watson, *Encelia farinosa*, and cacti, including *Echinocereus engelmannii* (Engelm.) Lem., *Opuntia basilaris* Engelm. & J. M. Bigelow and *O. echinocarpa* Engelm. & J. M. Bigelow (Steers and Allen 2011b). The slope at the study site was 5 to 6 degrees, facing east, at an elevation of about 525 m. Soils were alluvial (NRCS 2010) and about 80% sand (this study). Annual average precipitation is assumed to be between  $9.5 \pm 5.6$  SD and  $29.9 \pm 16.4$  SD cm, based on records for Palm Springs, about 19 km to the southeast, and Cabazon, about 14 km to the southwest, respectively (WRCC 2008). Precipitation at the Palm Springs weather station was 3.1, 4.8 and 16 cm for calendar years 2006, 2007 and 2008, respectively. Summer precipitation was negligible during these three years, which is typical for the area (WRCC 2008). Fire disturbance in this part of the Colorado Desert is not uncommon, and several burned stands of creosote bush scrub have been previously investigated nearby (O'Leary and Minnich 1981; Brown and Minnich 1986; Steers and Allen 2011b).

### Fire History Determination

The fire history of the study site was determined based on stereoscope validation of fire perimeters from a series of aerial photographs of the study landscape, spanning from 1949 to 2005. Aerial photos were obtained from Riverside County Flood Control and Water Conservation District, Coachella Valley Water District, and UC Riverside Science Library. The years when aerial photos were taken include the following: 1949, 1957, 1974, 1980, 1984, 1985, 1986, 1987, 1989, 1990, 1995, 1996, 1998, 2000, and 2005. For fires that occurred after the 2005 aerial photographs, additional fires were recorded from personal observation. Aerial photography revealed that the year of the first fire occurred sometime between 1987 and 1989. Because fires in desert vegetation are more common following winter seasons with above average rainfall (Brooks and Matchett 2006), the wettest year, which was 1988, is reported as the assumed burn year. Based on personal observations, the second fire occurred in the summer of 2005, following a winter of above average precipitation (WRCC 2008).

Based on aerial photography, the pattern of fire at the study site transformed an area with similar creosote bush shrub cover into three stands, one of which was a 1.7 ha remnant unburned stand, a 2.7 ha once-burned stand (burned in 1988), and a 3.3 ha twice-burned stand (burned in 1988 and 2005). At the time of both fires, fuel breaks (dozer-lines) were implemented to contain each fire from spreading into adjacent areas. Therefore, differences in vegetation among all three investigated stands prior to the first fire, and differences between the vegetation in the once- and twice-burned stands prior to the second fire, are assumed to be negligible.

### Soil and Vegetation Sampling

In August of 2006, six vegetation sampling plots were implemented in a stratified random design within each unburned, once-burned, and twice-burned vegetation stand. A sampling plot consisted of one, 7.32 m radius, modified – National Weed Management Association (mod-NAWMA) plot (Stohlgren et al. 2005). Slope and aspect were measured from the center of each plot using a compass and clinometer. Soil was collected to determine nutrient levels, physical characteristics, and to assess the seed bank. For soil nutrients, four soil samples per mod-NAWMA plot were taken to 5 cm depth with a 2.5 cm diameter corer and pooled into one composite sample per plot. The four samples were collected at the center and at three edge locations (7.32 m from plot center), at 30, 150, and 270 degrees from plot center. For soil seed bank samples, four cores per plot were also collected within a 20 cm radius of the soil nutrient sample plugs,

except 5 cm diameter cores were used instead. These cores were also pooled into one composite sample per plot. One core with the same dimensions used for seed bank samples was taken at the center of the plot, within a 20 cm radius of where the other soil samples were collected, for bulk density, coarse fraction (>2 mm), and soil texture measures. All soil sampled was taken at a 5 cm depth and placed in one of three plastic Ziploc bags per plot, for soil nutrient, seed bank, and physical (bulk density, coarse fraction, and soil texture) measurements, and then transported back to UC Riverside. At UC Riverside, samples taken with the 2.5 cm diameter corer were split, and 50 g were used to measure pH in a 1:1 soil:water slurry using a Fisher Scientific® Model 50 pH meter. The remaining portion of the soil nutrient samples were then sent to the University of California, Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis for carbon (C), total nitrogen (N), KCl-extractable  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , and texture (% sand, silt and clay) analyses (<http://groups.ucanr.org/danranlab>).

Soil seed bank samples were assayed by growing them out in a glasshouse and counting the number of germinants per species (Cox and Allen 2008). First, a composite sample was sieved through a 6 mm  $\times$  6 mm mesh to remove coarse materials, making sure not to remove any seeds, and then spread out on a 20 cm  $\times$  20 cm styrofoam tray. Soil depth in each tray ranged from 1 cm to 2 cm. Then, trays were kept moist and germinants were removed when identifiable or at a stage where they could be transplanted safely to pots to await identification. Watering continued in all trays until no new seeds germinated and then trays were left to dry. Once the soil in each tray was completely dry, it was mixed before the next watering cycle. Three cycles of watering and drying took place from September 2007 to May 2008. Trays were allowed to dry from 3 to 6 weeks between watering periods. By the third cycle, negligible numbers of seeds germinated so further cycles were not implemented. Throughout the watering, trays were reorganized several times to minimize localized effects within the glasshouse.

During the winter wet-season of 2006–07, insufficient rainfall prevented the germination of annual plants at the study site, and no vegetation measurements were taken. In the winter of 2007–08, precipitation was about average and vegetation was sampled in March 2008 during peak-flowering. In each established mod-NAWMA plot, percent cover by species was measured in three 1 m<sup>2</sup> (1 m  $\times$  1 m) quadrats, located 4.57 m from plot center at 30, 150, and 270 degrees. Species richness was measured within each of the three 1 m<sup>2</sup> quadrats per plot and also within each plot (out to a 7.32 m radius from plot center). All species names follow nomenclature in Hickman (1996).

## Data Analyses

Annual plant composition between the three stands (unburned, once-burned, and twice-burned) was compared using presence/absence data for all annual species recorded in the six mod-NAWMA plots per stand. Plots were ordinated with Nonmetric Multidimensional Scaling using a Sorenson distance measure (McCune and Mefford 2006). A random starting configuration with 50 runs of real data was used in the autopilot mode with medium speed. Then, a Multiresponse Permutation Procedure, using a Sorenson distance measure, was performed on the same data to determine if there were any significant pairwise difference between annual species composition in the three stands at  $\alpha = 0.05$  (McCune and Mefford 2006).

Other comparisons between the three stands were also conducted based on categorizations of species (e.g., native versus invasive), species richness, and species similarity indices. Annual vegetation cover was categorized into invasive grass, invasive forb, total invasive annuals (grass + forb), and native annuals (grass + forb) at the 1 m<sup>2</sup> scale (in quadrats). Native annual grasses and forbs were combined and not treated separately because the number of native annual grass species was very low (Appendix 1). Species richness of native annuals was calculated at both the quadrat and mod-NAWMA plot scales while species richness of herbaceous perennials and shrubs were only calculated at the mod-NAWMA plot scale. To determine the impact of fire on seed banks, germinants were grouped into four categories: invasive grasses, invasive forbs, native annuals, and shrubs plus cacti. No herbaceous perennials were found in the seed bank assays.

Shannon Diversity ( $H'$ ) was calculated at the quadrat scale based on native annual richness and cover by species (Shannon and Weaver 1963). Also, within-plot native annual plant species similarity ( $S$ ) was also calculated from the three 1 m<sup>2</sup> quadrats per mod-NAWMA plot. This was done using a multiple-quadrat community coefficient based on a modification of the Sorenson index (Diserud and Ødegaard 2007):  $S = (3/2)[ab + ac + bc - abc]/[a + b + c]$ , where  $a$  is the number of species in quadrat (plot frame) A,  $b$  is the number of species in quadrat B, etc... and  $ab$ ,  $ac$ ,  $bc$  and  $abc$  are the number of species shared between quadrats A and B, A and C, B and C and A, B and C, respectively.

To improve the normality of data, germinant density and native annual plant richness were square-root transformed. One-way ANOVA and Fisher's LSD test were used to compare the soil and vegetative variables among unburned, once-burned, and twice-burned conditions at  $\alpha = 0.05$ . Vegetation parameters that were constituted of more than one sub-sample per mod-NAWMA

TABLE 1. AVERAGE SOIL AND PERENNIAL PLANT PARAMETERS FOUND IN UNBURNED, ONCE-BURNED (1988), AND TWICE-BURNED (1988 AND 2005) STANDS. For each parameter, F test statistics based on one-way ANOVA are shown. Differences in superscript letters indicate significant differences between stands based on post-hoc LSD tests. Parameters that did not differ significantly between paired stands do not contain letter superscripts.  $n = 6$  and  $\alpha = 0.05$  for all statistical analyses.

Parameters	Unburned (avr. $\pm$ SE)	Once-burned (avr. $\pm$ SE)	Twice-burned (avr. $\pm$ SE)	F
<b>SOIL</b>				
Total N (%)	0.08 $\pm$ 0.01 <sup>A</sup>	0.10 $\pm$ 0.01 <sup>AB</sup>	0.13 $\pm$ 0.01 <sup>B</sup>	5.6115
Total C (%)	0.75 $\pm$ 0.09 <sup>A</sup>	0.96 $\pm$ 0.07 <sup>AB</sup>	1.23 $\pm$ 0.11 <sup>B</sup>	6.8488
NH <sub>4</sub> <sup>+</sup> (ppm)	13.1 $\pm$ 1.3	13.7 $\pm$ 1.4	14.2 $\pm$ 2.1	0.1046
NO <sub>3</sub> <sup>-</sup> (ppm)	11.3 $\pm$ 1.9	11.9 $\pm$ 1.2	14.6 $\pm$ 2.1	0.9811
Sand (%)	77.8 $\pm$ 1	80 $\pm$ 1.1	80.5 $\pm$ 0.8	2.1964
Silt (%)	17 $\pm$ 0.7	16.7 $\pm$ 1	15 $\pm$ 0.7	1.8023
Clay (%)	5.2 $\pm$ 0.5 <sup>A</sup>	3.3 $\pm$ 0.4 <sup>B</sup>	4.5 $\pm$ 0.2 <sup>AB</sup>	5.6707
pH	7.4 $\pm$ 0.1 <sup>A</sup>	7.6 $\pm$ 0 <sup>B</sup>	7.7 $\pm$ 0 <sup>B</sup>	9.1424
Bulk density (g/cm <sup>3</sup> )	1.29 $\pm$ 0.09	1.15 $\pm$ 0.06	1.15 $\pm$ 0.08	1.0887
Coarse fraction (g/cm <sup>3</sup> )	0.31 $\pm$ 0.03	0.42 $\pm$ 0.13	0.49 $\pm$ 0.03	1.3802
Bare ground cover (%)	7.1 $\pm$ 2.2 <sup>A</sup>	12.3 $\pm$ 5.3 <sup>AB</sup>	18.9 $\pm$ 3.4 <sup>B</sup>	2.4091
Rock cover (%)	3.4 $\pm$ 1.5 <sup>A</sup>	5.7 $\pm$ 2 <sup>A</sup>	12.1 $\pm$ 2.5 <sup>B</sup>	4.8556
Litter cover (%)	3.7 $\pm$ 1.1	5.8 $\pm$ 2.9	1.6 $\pm$ 0.6	1.3029
<b>HERBACEOUS PERENNIALS</b>				
Richness (species/168.3 m <sup>2</sup> )	0.8 $\pm$ 0.4	0 $\pm$ 0	0.5 $\pm$ 0.3	1.9000
<b>SHRUBS</b>				
Richness (species/168.3 m <sup>2</sup> )	6 $\pm$ 0.5 <sup>A</sup>	2 $\pm$ 0.5 <sup>B</sup>	1.2 $\pm$ 0.2 <sup>B</sup>	46.8182
Live cover (%)	10.6 $\pm$ 3	18.6 $\pm$ 9.3	18.6 $\pm$ 5.1	0.5323
<i>Encelia farinosa</i> cover (%)	0 $\pm$ 0 <sup>A</sup>	17.9 $\pm$ 9.4 <sup>B</sup>	16.4 $\pm$ 4.8 <sup>B</sup>	2.6668

plot (e.g., percent cover and species richness per m<sup>2</sup>) were averaged together before analyses. Thus, for all soil and vegetation analyses,  $n = 6$ . Similar statistical procedures have been utilized when comparing paired burned and unburned vegetation in low replication contexts (Haidinger and Keeley 1993; Brooks and Matchett 2003; Abella et al. 2009).

## RESULTS

### Impact of Fire on Soils

Some soil parameters were influenced by fire while others were not (Table 1). Extractable nitrogen (NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>) did not differ between paired burned and unburned areas. However, total N and C, and soil pH were greater in the twice-burned area than the unburned area. Also, percent cover of bare ground and rock were greatest in the twice-burned area (Table 1).

### Impact of Fire on Seed Banks

A total of 6357 germinants belonging to 14 species were recorded from the seed bank study. About 97% of the seed bank germinants were *Schismus barbatus* and *S. arabicus*, which are collectively referred to as *Schismus* spp. Invasive forbs, *Erodium cicutarium* and *Brassica tournefortii* Gouan, made up about 0.6%, with 29 and 12 individuals counted, respectively. Only four *Bromus madritensis* ssp. *rubens* individuals were

counted, all of which only occurred in soils from the unburned area. Eight native annual species made up about 1.8% of the total germinants counted. The most abundant native species were *Camissonia californica* (Torr. & A. Gray) P. H. Raven, *Crassula connata* (Ruiz & Pav.) A. Berger, and *Plantago ovata* Forssk. Only *Encelia farinosa* and one unknown cactus that died prematurely made up the six germinants in the shrub plus cacti category.

Analyses of the seed bank at a scale of 78.5 cm<sup>2</sup> showed that the twice-burned stand had greater invasive annual grass density than the once-burned and unburned stands (Fig. 1). No differences in invasive forb and native annual germinants were found between stands (Fig. 1). At this small scale, mean native annual plant richness also was not different between the unburned (1.33  $\pm$  0.33 SE species), once-burned (1  $\pm$  0.52 SE), and twice-burned (1.33  $\pm$  0.33 SE) stands.

### Impact of Fire on Aboveground Vegetation

Five exotic annuals and 38 native annual species (Appendix 1) were documented. Of the exotics encountered, the invasive forbs, *Brassica tournefortii* and *Erodium cicutarium*, were widespread in all three areas, as were the invasive grasses, *Schismus* spp. When comparing annual plant species composition among the three paired stands, the Nonmetric Multidimensional Scaling (NMS) analysis resulted in a two-dimensional solution.

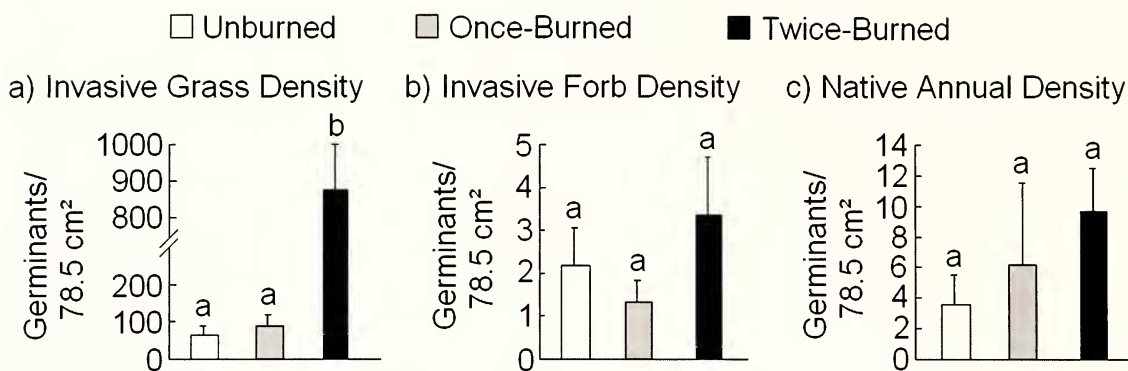


FIG. 1. Average density and SE bars for invasive grass (a), invasive forb (b), and native annual (c) germinants from seed bank assays of the unburned, once-burned, and twice-burned stands. Differences in letters above bars indicate significant differences between stands based on ANOVA and LSD tests ( $\alpha = 0.05$ ).

The final stress for the best solution was low, at 12.23 out of 100. The proportion of variance represented by each axis, based on the  $r^2$  between distance in the ordination space and distance in the original space was 0.681 and 0.209 for axis 1 and 2, respectively. Thus, the separation that was revealed among the three stands was primarily along axis 1 (Fig. 2). Species that had the strongest correlation with axis 1 were *Bromus madritensis* ssp. *rubens* ( $r = -0.851$ ), *Chaenactis fremontii* A. Gray ( $r = -0.841$ ), *Vulpia octoflora* (Walter) Rydb. ( $r = -0.819$ ), *Pectocarya linearis* DC. ( $r = -0.696$ ), *Stylocline gnaphaloides* Nutt. ( $r = -0.658$ ), *Pholistoma membranaceum* (Benth.) Constance ( $r = -0.653$ ), and *Phacelia distans* Benth. ( $r = -0.652$ ). When the three stands were compared using the Multi-Response Permutation Procedure, the unburned stand had a significantly different annual plant community than the once-burned ( $A = 0.296$ ;  $P < 0.001$ ) and twice-burned ( $A = 0.299$ ;  $P < 0.001$ ) stands. Similarly, the

once-burned and twice-burned stands were also significantly different from each other ( $A = 0.134$ ;  $P < 0.001$ ).

No difference in total invasive annual plant cover between the unburned, once-burned and twice-burned stands was detected (Fig. 3). However, invasive grass cover was greater and invasive forb cover was lower in the twice-burned compared to the once-burned stand (Fig. 4). In addition, relative cover of invasive grasses was greatest in the twice-burned stand versus the other two stands (Fig. 3). Native annual plant cover and species richness at the 1 m<sup>2</sup> scale were lower in both of the burned stands compared to the unburned stand (Figs. 3 and 4). Also at the 1 m<sup>2</sup> scale, the stand that had burned twice did not have lower native cover or richness compared to the stand that had only burned once. However, native annual plant diversity (Shannon Diversity -  $H'$ ) was lower in the twice-burned stand compared to the other two stands (Fig. 3). Also, only in the twice-burned stand was within-plot native annual plant similarity (based on shared species among the three 1 m<sup>2</sup> quadrats per plot) greater than the unburned stand (Fig. 3). In other words, the variety of annual species found in twice-burned vegetation was lower compared to the unburned stand. At a larger scale (168.3 m<sup>2</sup> mod-NAWMA plot), native annual species richness was lower within each burned stand (Fig. 3). Also at this larger scale, shrub richness was lower for the first burn, but showed no further decrease after the second burn. Herbaceous perennial richness was very low in general and did not differ among the three stands (Table 1).

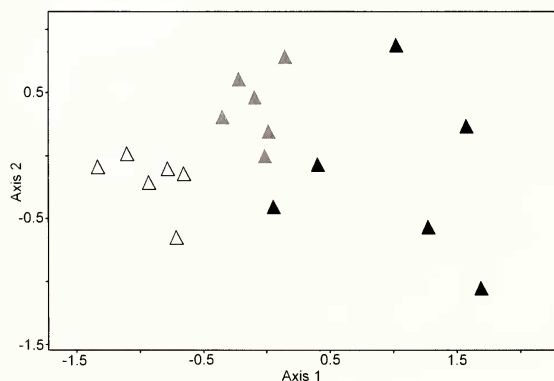


FIG. 2. A Nonmetric Multidimensional Scaling ordination of unburned, once-burned, and twice-burned sample units (white, grey, and black triangles, respectively) based on presence/absence of annual species recorded in 168.3 m<sup>2</sup> mod-NAWMA plots.

## DISCUSSION

### Impact of Fire on Soils

Soil pH, and total N and C were greatest in the twice-burned stand, which last experienced fire three years prior to sampling. Elevated pH is

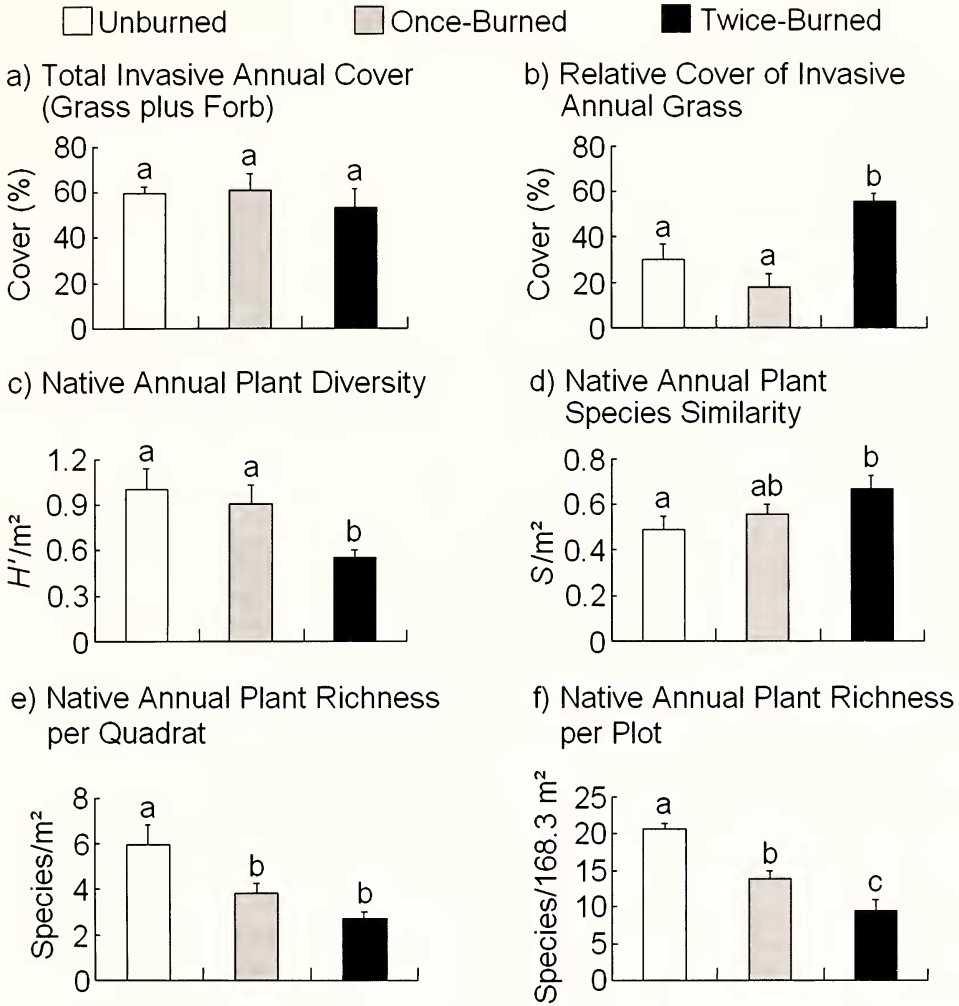


FIG. 3. Invasive annual plant cover (a), relative invasive annual grass cover (b), and various native annual plant diversity measures: Shannon index (c), Sørensen index (d), richness per 1  $m^2$  quadrat (e), and richness per 168.3  $m^2$  mod-NAWMA plot (f). Values in each graph are averages per stand with SE bars. Differences in letters between paired stands within each graph indicate significant differences at  $\alpha = 0.05$ .

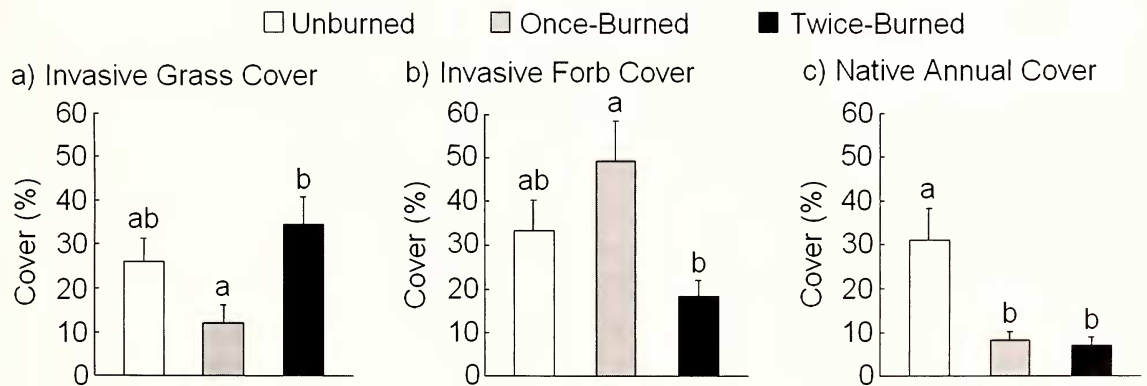


FIG. 4. Average cover and SE bars for invasive grasses (a), invasive forbs (b), and native annuals (c) in the unburned, once-burned, and twice-burned stands. Differences in letters above bars indicate significant differences between stands per graph based on ANOVA and LSD tests ( $\alpha = 0.05$ ).

common following fire due to increased ash (Raison 1979; Abella et al. 2009). The response of total N and C to fire, however, is variable (Raison 1979; Brooks 2002; Allen et al. 2011). Pre-fire *Encelia* cover was assumed to be high in the twice-burned stand based on conditions in the once-burned stand, which likely accounts for the elevated C and N found in post fire soils (Xie and Steinberger 2001). Soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were highest in the twice-burned stand but not significantly so. These mobile, inorganic forms of nitrogen are typically elevated in post-fire environments (Wan et al. 2001), even in creosote bush scrub (Esque et al. 2010b). It is possible that both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were significantly elevated immediately after the 2005 fire in the twice-burned stand but by the time the sites were sampled in August of 2006, these nitrogen sources had decreased due to leaching and/or immobilization.

Post-fire bare ground and rock cover was elevated in the twice-burned stand. Adams et al. (1970) reported higher bare ground after fire in creosote bush scrub of the Colorado Desert due to hydrophobic soils that were characterized by water repellent layers found at various depths under burned shrubs. Large bare areas under burned shrubs, as they described, were not observed during this study. In general, the altered soil properties that resulted from fire were not dramatic and are expected to return to pre-fire conditions as vegetation recovers (Allen et al. 2011). However, persistent invasive species, a continuation of a short fire return interval or heightened soil erosion could cause long-term alterations to soil properties (Morris and Moses 1987; Belnap 1995; Allen et al. 2011).

#### Impact of Fire on Seed Bank Germinants

In general, propagule abundance is linked to above ground plant performance (Olano et al. 2005; Cox and Allen 2008). Therefore, seed bank composition can elucidate potential aboveground vegetation, especially in the context of future disturbances (Cox and Allen 2008; Satterthwaite et al. 2007; Fisher et al. 2009). Results from the seed bank assays revealed that invasive grass propagules of *Schismus* spp. are ubiquitous and abundant in the seed bank at this site. Future fires or other disturbances will likely promote these plants (Cox and Allen 2008; Fisher et al. 2009). Native species also did not differ among stands, which suggests that invasive species removal could be an effective strategy for native seed bank management, especially because native annual plants exhibit density dependent inhibition of germination (Inouye 1980).

When scaled up, the number of invasive annual grass propagules in the twice-burned stand was  $111,952.9 \pm 15,760$  SE per  $\text{m}^2$ . To our knowledge, this is vastly greater than any value

previously reported for exotic annual grasses from the American southwest (Young and Evans 1975; Nelson and Chew 1977; Reichman 1984; Hassan and West 1986; Guo et al. 1998; Ango-Roman et al. 2005; Cox and Allen 2008; Abella et al. 2009; Esque et al. 2010a). The relative lack of other germinants besides *Schismus* spp. may indicate that the methods used to assay the seed bank were not ideal for detecting the full suite of species that could occur in the seed bank. Native desert annuals, in particular, are known to exhibit high interannual variation (Freas and Kemp 1983; Philippi 1993; Pake and Venable 1996). While multiple watering cycles were utilized to address this potential variation, and while *Schismus* germinants were removed immediately to minimize interference, it is possible that not all viable native seeds in the seed bank samples germinated during the assays. For example, Esque et al. (2010a) treated seed bank samples with gibberellic acid to stimulate germination and observed native annual germinants to be magnitudes greater than what we found.

#### Impact of Fire on Annual Plants

Invasive annual grasses and forbs can severely reduce the abundance and species richness of native annual plants in unburned vegetation (Huenneke et al. 1990; Crimmins and McPherson 2008; Davies and Svejcar 2008; Minnich 2008). This study suggests that fire disturbance is also a serious threat to native annuals because it promotes invasive plants like *Schismus* spp. Abundance of *Bromus madritensis* ssp. *rubens* typically decreases in the immediate post-fire years (Abella et al. 2009; Esque et al. 2010a) although it is expected to return to or even exceed pre-fire abundance levels within three years after fire, if precipitation is adequate (Brooks 2003). The mechanism whereby *Schismus* spp. increases immediately after fires relates to the small size of its seeds, which fall into cracks and escape damage from fire, plus its ability to take advantage of elevated inorganic nitrogen levels in the post-fire environment (Esque et al. 2010b). Because nitrogen-use traits may not differ between invasive and native annuals, the relative early germination and more rapid phenology of *Schismus* spp. contributes to its success (Marushia et al. 2010; Steers et al. 2011).

At this study site, fire reduced the quadrat- and plot-level species richness of native annual plants, and recurrent fire magnified this outcome at the plot-level. Recurrent fire also significantly decreased species diversity, which led to a highly simplified assemblage of annual plants in the twice-burned stand. Despite the negative impact of fire on native annuals, if invasive annuals are removed post-fire, then native annual species

richness can increase greatly, likely exceeding pre-fire levels (Steers and Allen 2010, 2011c).

### Relevance to the Grass/Fire Cycle

At our study site, invasive annual grass cover within the first three years after a fire was greater in the burned compared to the unburned stand, due almost entirely to *Schismus* spp., which is similar to other studies (Cave and Patten 1984; Minnich and Dezzani 1998; Brooks 2002; Esque et al. 2010b; Steers and Allen 2011a). This difference in invasive annual grasses may translate to greater potential for a consequent fire (Brooks et al. 2004). *Schismus* spp. are generally considered less effective at carrying fire than larger annual grasses like *Bromus madritensis* ssp. *rubens* (Brooks 1999). However, in this region *Schismus* spp. can attain relatively large sizes due to high anthropogenic nitrogen deposition, especially in wet years (Rao and Allen 2010; Rao et al. 2010) and are known to carry stand-replacing fires. For example, in the summer of 2005, at least four other creosote bush scrub fires within a 10 km radius of the study site were primarily fueled by *Schismus* spp. (R. Steers personal observations). Therefore, given adequate precipitation, results from this study suggest that fire can promote invasive annual grasses (i.e., *Schismus* spp.), which in turn, could fuel additional fires in a positive feedback, as described by the grass/fire cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004).

### Management Implications

Removal of invasive grasses and forbs should favor natives through decreased competition (Brooks 2000; Schutzenhofer and Valone 2005; Barrows et al. 2009; Steers and Allen 2010) and through limiting future fire disturbance (Brooks et al. 2004). Because native annual richness is linked to the spatial and structural heterogeneity of creosote bush scrub (Schmidha and Whittaker 1981), some native species may not find suitable micro-habitats until the shrub components are returned, regardless of invasive plant removal. For example, *Pholistoma membranaceum* was the most abundant annual forb in the unburned stand (Appendix 1) where it occurred almost exclusively in shrub understories of long-lived species, like *Larrea tridentata* (R. Steers personal observation). *Pholistoma membranaceum* was virtually eliminated in the once-burned and twice-burned stands even though *Encelia farinosa* shrubs were prevalent. Unfortunately, reestablishment of long-lived shrubs, like *Larrea tridentata*, has been speculated to take decades or longer (Vasek 1983; Lovich and Bainbridge 1999; Abella 2009, 2010; Steers and Allen 2011b). Because of invasive species and the long time scale required for desert vegetative succession,

intervention through restoration practices may be required to ensure the return of certain native annual species, although this may only be feasible at small scales or where special status plant species are at risk.

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APPENDIX 1. Average cover of each annual species recorded per quadrat (1 m<sup>2</sup>) and their respective frequency score per stand (unburned, once-burned, or twice-burned stands). Frequency is the number of occurrences per six 168.3 m<sup>2</sup> mod-NAWMA plots per stand.

Family	Species	Unburned	Once-burned	Twice-burned
		Cover (%)/ frequency per six plots	Cover (%)/ frequency per six plots	Cover (%)/ frequency per six plots
<b>INVASIVE FORBS</b>				
Brassicaceae	<i>Brassica tournefortii</i> Gouan	22.1/6	41.9/6	5.2/6
Geraniaceae	<i>Erodium cicutarium</i> (L.) Aiton	11.2/6	7.3/6	13.4/6
<b>INVASIVE GRASSES</b>				
Poaceae	<i>Bromus madritensis</i> L. subsp. <i>rubens</i> (L.) Husn.	4.1/6	<0.1/6	0/3
	<i>B. tectorum</i> L.	0/4	<0.1/1	<0.1/1
	<i>Schismus barbatus</i> (L.) Thell. and <i>S. arabicus</i> Nees	22.1/6	11.9/6	34.7/6
<b>NATIVE ANNUALS</b>				
Asteraceae	<i>Chaenactis fremontii</i> A. Gray	5.7/6	0.8/6	0/2
	<i>Filago californica</i> Nutt.	0.6/6	0/5	0.2/4
	<i>F. depressa</i> A. Gray	<0.1/2	0/0	0/0
	<i>Lasthenia californica</i> Lindl.	<0.1/5	0/3	<0.1/5
	<i>Malacothrix glabrata</i> A. Gray	0/0	0/3	0.2/3
	<i>Rafinesquina neomexicana</i> A. Gray	0.1/6	0/0	0/0
	<i>Stephanomeria exigua</i> Nutt.	0/0	0/0	<0.1/2
	<i>Stylochne gnaphaloides</i> Nutt.	1.4/6	0/1	0/0
	<i>Uropappus lindleyi</i> (DC.) Nutt.	0/0	<0.1/1	0/1
Boraginaceae	<i>Amsinckia menziesii</i> A. Nelson & J. F. Macbr.	1/6	0/1	0/1
	<i>Cryptantha barbigera</i> Greene	0/5	0.8/6	1/5
	<i>Pectocarya heterocarpa</i> I. M. Johnst.	0.3/5	0/0	0/0
	<i>P. linearis</i> DC.	0.7/5	<0.1/5	<0.1/1
	<i>P. recurvata</i> I. M. Johnst.	0.8/5	0.1/5	0/2
Brassicaceae	<i>Descurainia pinnata</i> (Walter) Britton	0/0	<0.1/3	0/1
	<i>Lepidium lasiocarpum</i> Torr. & A. Gray	0/0	0/3	<0.1/1
	<i>Tropidocarpum gracile</i> Hook.	0/1	0/0	0/0
Caryophyllaceae	<i>Loeflingia squarrosa</i> Nutt.	<0.1/5	0/0	0/0
Crassulaceae	<i>Crassula connata</i> (Ruiz & Pav.) A. Berger	1.3/6	0.1/4	<0.1/4
Fabaceae	<i>Lotus strigosus</i> (Nutt.) Greene	<0.1/5	0/0	<0.1/1
	<i>Lupinus sparsiflorus</i> Benth.	0/2	0/0	0/0
Hydrophyllaceae	<i>Emmenanthe penduliflora</i> Benth.	0.1/6	3.3/6	2.5/6
	<i>Phacelia campanularia</i> A. Gray	0/0	0/2	<0.1/2
	<i>P. distans</i> Benth.	1.4/5	<0.1/6	0/0
	<i>Pholistoma membranaceum</i> (Benth.) Constance	13.2/6	0/1	0/0
Lamiaceae	<i>Salvia columbariae</i> Benth.	0/0	0/0	0/1
Loasaceae	<i>Mentzelia involucrata</i> S. Watson	0/0	0/1	0/0
	<i>Mentzelia</i> sp.	<0.1/2	0/0	0/0
Onagraceae	<i>Camissonia californica</i> (Torr. & A. Gray) P. H. Raven	0.1/6	1.1/6	2/6
	<i>C. pallida</i> (Abrams) P. H. Raven	0.1/4	0/2	<0.1/4
Plantaginaceae	<i>Plantago ovata</i> Forssk.	0.1/6	0.7/6	1.1/3
Poaceae	<i>Vulpia microstachys</i> (Nutt.) Benth.	0/1	0/0	0/0
	<i>V. octoflora</i> (Walter) Rydb.	3.9/6	0.9/6	0/1
Polemoniaceae	<i>Gilia angelensis</i> V. E. Grant	0.2/1	0/0	0/0
	<i>Linanthus bigelovii</i> Greene	0/2	0/0	0/0
Polygonaceae	<i>Chorizanthe brevicornu</i> Torr.	0/2	0/0	0/0
	<i>Pterostegia drymarioides</i> Fisch. & C. A. Mey.	0/1	0/0	0/0
Portulacaceae	<i>Calyptridium monandrum</i> Nutt.	0/0	0/1	0/1